

DAYTIME SURFACE SWARMS OF *THYSANOESSA SPINIFERA*
(EUPHAUSIACEA) IN THE GULF OF THE
FARALLONES, CALIFORNIA

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ABSTRACT

Daytime surface swarms of the euphausiid *Thysanoessa spinifera* were observed and sampled in spring 1985 in the Gulf of the Farallones off San Francisco, California. Samples were dipnetted at the surface from nine discrete swarm patches; and depth-stratified plankton tows were made before, during, and after swarm activity. Analyses of sex and maturity stage of surface patch samples showed that 94% of all euphausiids were in breeding condition. Sex ratios differed significantly in six of the nine patches, with males dominating four and females dominating two patches. This sexual segregation is thought to be related to differences in size between sexually mature males and females. Biological and oceanographic observations at the swarm site, and examinations of food baskets of swarm individuals, gave little indication that the animals were passively transported to the surface, or that they were there to feed or avoid predators. *T. spinifera* eggs and Stage I nauplii were numerous in plankton collections taken the night following, and day after surface swarming was observed. It is concluded that swarming in this species is related to reproduction. Its adaptive value in regard to different breeding-related activities is still unclear, but probably involves a combination of factors that relate to the timing of sexual maturation, egg release, and larval dispersal in the changeable upwelling environment off central California.

The neritic euphausiid *Thysanoessa spinifera* aggregates in conspicuous daytime swarms at the ocean surface along the California coast during spring and summer. Little is known about these surface swarms or what triggers their formation, probably because of the unpredictable nature of their onset and duration. The behavior occurs during daylight when most vertically migrating euphausiids, including *T. spinifera* (Alton and Blackburn, 1972), are usually found at greater depths.

In general, upwelling centers have been associated with highest densities of *T. spinifera* (Brinton, 1962); and in the Gulf of the Farallones, daytime swarms occur sporadically from about April to July, when upwelling events are the most frequent and intense along the central California coast (Bakun, 1975). During this time, northwest winds intensify, triggering the offshore transport of warm surface waters, which are then replaced by cool, nutrient-rich water from the depths (Bolin and Abbot, 1962). Periodically during the upwelling season, northwesterly winds slacken, the process temporarily subsides, and surface temperatures may rise due to solar radiation or intrusion of warmer offshore water (Bolin and Abbot, 1962; Hatfield, 1983).

When the rust-colored patches appear, many of the commercial sport fishing boats, guided by flocks of feeding seabirds, seek them out in search of salmon, which we have found to feed heavily on euphausiids at this time of year. Although this daytime swarming is often highly visible and appears to be a relatively common event off central California, very little information is available on swarm population structure. The only published reports consist of brief accounts of swarms that washed ashore at La Jolla, California (Boden et al., 1955), and Bandon, Oregon (Percy and Hosie, 1985), which were composed entirely of spent females, and those observed in Monterey Bay by Barham (1956) for which sex and maturity composition are not known.

- Simpson, J. J. 1987. Transport processes affecting the survival of pelagic fish stocks in the California Current. *Amer. Fish. Soc. Symp.* 2:39-60.
- Smith, P. E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. *Fish. Bull., U. S.* 70:849-874.
- . 1978. Biological effects of ocean variability: time and space scales of biological response. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* 173:117-127.
- . 1985a. Year-class strength and survival of O-group clupeoids. *Can. J. Fish. Aquat. Sci.* 42 (Suppl. 1): 69-82.
- . 1985b. A case history of an anti-El Niño transition on plankton and nekton distribution and abundances. In *El Niño north: El Niño effects in the eastern subarctic Pacific Ocean*, W. S. Wooster and D. L. Fluharty, eds. Washington Sea Grant Program, pp. 121-142.
- Smith, P. E., and R. W. Eppley. 1982. Primary production and the anchovy population in the Southern California Bight: comparison of time series. *Limnol. Oceanogr.* 27:1-17.
- Soutar, A., and J. D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments off the Californias. *Fish. Bull., U. S.* 72:257-273.
- Stauffer, G. D., and R. L. Charter. 1982. The northern anchovy spawning biomass for the 1981-82 California fishing season. *Calif. Coop. Oceanic Fish. Invest. Rep.* 23:15-19.
- Stauffer, G. D., and S. J. Picquelle. 1981. Estimate of the spawning biomass of the northern anchovy central subpopulation for the 1980-81 fishing season. *Calif. Coop. Oceanic Fish. Invest. Rep.* 22:8-13.
- Stevens, E. G., and H. G. Moser. 1982. Observations on the early life history of the mussel blenny, *Hypsoblennius jenkinsi*, and the bay blenny, *Hypsoblennius genivittatus*, from specimens reared in the laboratory. *Calif. Coop. Oceanic Fish. Invest. Rep.* 23:269-275.
- Sumida, B., E. H. Ahlstrom, and H. G. Moser. 1979. Early development of seven flatfishes of the eastern North Pacific with heavily pigmented larvae (Pisces, Pleuronectiformes). *Fish. Bull., U.S.* 77:105-145.
- Sumida, B. Y., H. G. Moser, and E. H. Ahlstrom. 1985. Descriptions of larvae of California yellowtail, *Seriola lalandi*, and three other carangids from the eastern tropical Pacific: *Chloroscombrus orqueta*, *Caranx caballus*, and *Caranx sexfasciatus*. *Calif. Coop. Oceanic Fish. Invest. Rep.* 26:139-159.
- Walker, H. J., Jr., W. Watson, and A. M. Barnett. 1987. Seasonal occurrences of larval fishes in the nearshore Southern California Bight off San Onofre, California. *Estuarine Coastal Shelf Sci.* 25: 91-109.
- Wolf, P., P. E. Smith, and C. L. Scannell. 1987. The relative magnitude of the 1986 Pacific sardine spawning biomass off California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 28:21-26.

APPENDIX

CalCOFI Ichthyoplankton Data Reports

- Ambrose, D. A., R. L. Charter, H. G. Moser, and C. R. Santos Methot. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1951*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 79, 196 pp.
- Sandknop, E. M., R. L. Charter, H. G. Moser, and J. D. Ryan. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1952*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 80, 207 pp.
- Stevens, E. G., R. L. Charter, H. G. Moser, and M. S. Busby. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1953*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 81, 186 pp.
- Sumida, B. Y., R. L. Charter, H. G. Moser, and D. L. Snow. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1954*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 82, 207 pp.
- Ambrose, D. A., R. L. Charter, H. G. Moser, and C. R. Santos Methot. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1955*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 83, 185 pp.
- Stevens, E. G., R. L. Charter, H. G. Moser, and M. S. Busby. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1956*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 84, 189 pp.
- Sumida, B. Y., R. L. Charter, H. G. Moser, and D. L. Snow. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1957*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 85, 225 pp.
- Sandknop, E. M., R. L. Charter, H. G. Moser, and J. D. Ryan. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1958*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 86, 248 pp.
- Stevens, E. G., R. L. Charter, H. G. Moser, and M. S. Busby. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1959*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 87, 273 pp.
- Ambrose, D. A., R. L. Charter, H. G. Moser, and C. R. Santos Methot. 1987. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1960*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 88, 253 pp.
- Sandknop, E. M., R. L. Charter, H. G. Moser, C. A. Meyer, and A. E. Hays. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1961*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 92, 167 pp.
- Sumida, B. Y., R. L. Charter, H. G. Moser, and D. L. Snow. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1962*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 93, 179 pp.
- Ambrose, D. A., R. L. Charter, H. G. Moser, and B. S. Earhart. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1963*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 94, 209 pp.
- Sandknop, E. M., R. L. Charter, H. G. Moser, C. A. Meyer, and A. E. Hays. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1964*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 95, 222 pp.
- Stevens, E. G., R. L. Charter, H. G. Moser, and L. R. Zins. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1965*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 96, 220 pp.
- Sumida, B. Y., R. L. Charter, H. G. Moser, and D. L. Snow. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1966*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 97, 287 pp.
- Ambrose, D. A., R. L. Charter, H. G. Moser, and B. S. Earhart. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1967*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 98, 103 pp.
- Sandknop, E. M., R. L. Charter, H. G. Moser, C. A. Meyer, and A. E. Hays. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1968*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 99, 112 pp.
- Stevens, E. G., R. L. Charter, H. G. Moser, and L. R. Zins. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1969*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 100, 265 pp.
- Sumida, B. Y., R. L. Charter, H. G. Moser, and D. L. Snow. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1972*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 109, 219 pp.
- Ambrose, D. A., R. L. Charter, H. G. Moser, and B. S. Earhart. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1975*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 110, 229 pp.
- Sandknop, E. M., R. L. Charter, H. G. Moser, C. A. Meyer, and A. E. Hays. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1978*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 111, 216 pp.
- Ambrose, D. A., R. L. Charter, H. G. Moser, and B. S. Earhart. 1988. *Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1981*. U.S. Dep. Commer., NOAA Tech. Memo., NMFS, SWFC, no. 112, 170 pp.

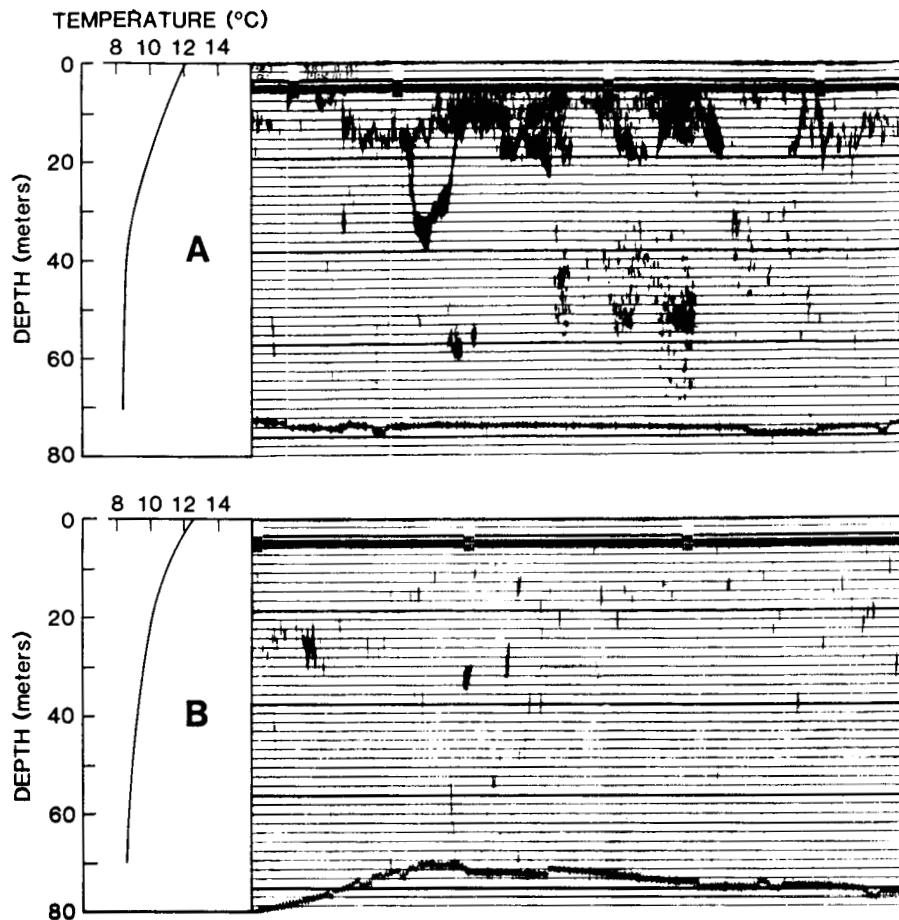


Figure 1A. Echogram (38 kHz) and XBT temperature profile obtained at the surface swarm site on the day of swarm observations, 31 May 1985; Figure 1B. Echogram and XBT temperature profile obtained at the surface swarm site the night following swarm activity, 1 June 1985.

drifted into the swarming area and during sampling. Some of the patches were roughly circular and contained tightly spaced individuals without parallel orientation. Others were ribbonlike streams of individuals, which swam parallel to each other at an estimated 0.3 m sec^{-1} . The animals often sounded rapidly as a group when disturbed, and some individuals even vaulted from the water in an effort to escape the dip net or the samplers' boat. Isolated individuals were also observed swimming at the surface outside the dense patches.

Although feeding activity of fishes has been associated with surface swarming of *T. spinifera* in Monterey Bay (Harvey³) and in the Gulf of the Farallones (by the salmon sportfishing fleet⁴), we saw no evidence of this at the swarm site. The

³ Harvey, J. T. Daytime surface swarming of euphausiids in Monterey Bay, California. Unpubl. manuscript, Hatfield Marine Science Center, Oregon State University, Newport, OR 97365.

⁴ Roger Thomas, Captain *Salty Lady*, Harbor Drive, Sausalito, CA 94965, pers. commun. May 1985.

Table 2. Estimated number per 1,000 m³ (N) and percent sample volume (%) of *T. spinifera* eggs, nauplii, and adults taken in plankton tows at the swarm site before, during, and after swarm activity

Tow depth (m)	Tow duration (min)	Eggs		Nauplii		Adults			Total sample volume (ml)
		N	%	N	%	Ripe ♂	Fert. ♀	%	
Night before swarm activity (0150–1340 hr)									
18	15	19,533	0.01	—	—	91	40	0.12	183
37	16	744	<0.01	—	—	18	10	0.05	94
55	15	689	<0.01	—	—	15	1	0.05	56
Day of swarm activity (1400 hr)									
55	15	3,217	<0.01	64	<0.01	—	*	—	109
Night following swarm activity (0200–0350 hr)									
18	15	17,235	0.05	—	—	3	3	0.01	63
37	15	28,151	0.20	—	—	—	2	0.01	43
55	15	18,269	0.13	—	—	1	1	0.01	31
Day after swarm activity (1240–1400 hr)									
18	15	4,600	0.01	1,181	<0.01	—	—	—	47
37	15	24,129	0.30	—	—	—	—	—	23
55	15	9,566	0.07	—	—	—	—	—	46

* A single, unfertilized female with early stage eggs was taken in this collection.

only predators evident in the area were western gulls (*Larus occidentalis*) which were observed on the water singly or in pairs, feeding on individual patches.

There was no evidence, either in our plankton collections (Table 2) or in echosounder tracings (Fig. 1B), that the surface swarming persisted after nightfall. Euphausiid eggs, however, were numerous in plankton collections taken that night and the next day (Table 2). Although positive identification could not be made of the eggs or of the Stage 1 nauplii found in near-surface samples the following day, the size of the egg embryos and the shape of the nauplii differed from those of *Euphausia pacifica*, the only other abundant euphausiid in the area.⁵ We therefore assume that the eggs and nauplii were those of *T. spinifera*. Egg numbers may have been underestimated because of possible extrusion through the net meshes (mean egg diameter = 0.41 mm; mesh width = 0.335 mm; mean diagonal mesh width = 0.42 mm).

Analyses of sex and maturity stage of the dipnetted samples from surface patches showed that 94% of all euphausiids were either males with fully developed spermatophores or fertilized females with ripe or ripening eggs. The sex ratio, however, differed from patch to patch. Six of the nine collections differed significantly from the expected 1:1 male : female ratio, with males dominating in four collections and females dominating in two collections (Table 1). Analyses of length frequencies by maturity stage helped to distinguish major components of the swarms (Fig. 2). Overall, sexually mature males (TL mean = 20.7 mm) and large fertilized females with eggs (TL mean = 25.4 mm) comprised 55.7% and 38.0%, respectively, of the sampled population. A third, lesser group (4.8% of individuals), which occurred strongly only in patch sample 2, was composed of smaller developing females (TL mean = 19.9 mm). The remainder (1.5%) consisted of unfertilized ripe females (8 individuals), spent females (6), and males without spermatophores (5).

⁵ Margaret Knight, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. March 1986.

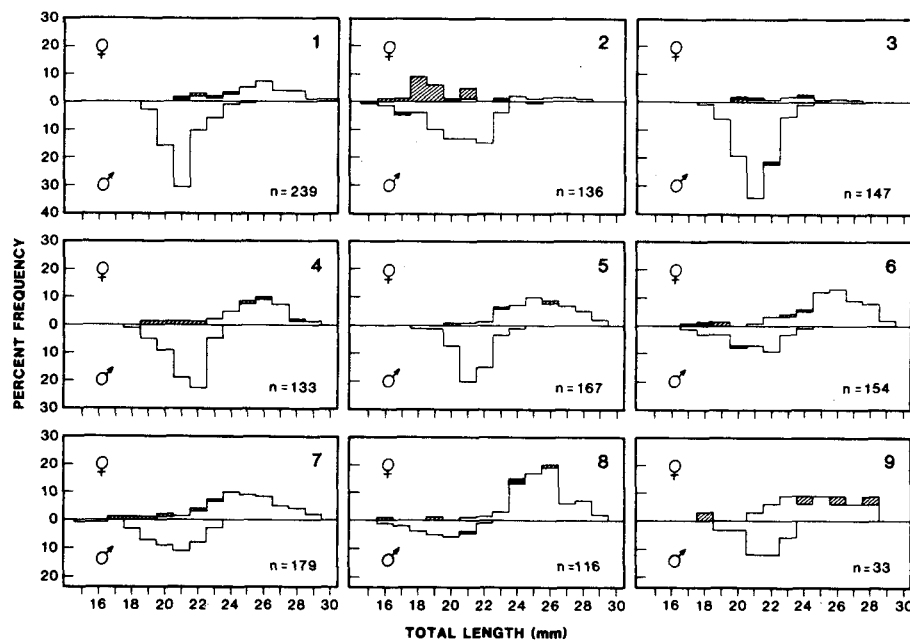


Figure 2. Length frequency histograms of the nine sampled swarm patches of *Thysanoessa spinifera*. Crosshatching = unfertilized developing females; open = fertilized females with ripe or ripening eggs and males with spermatophores; solid = other (males without spermatophores, fertilized females without eggs, and ripe, unfertilized females).

Examination of food baskets of swarm individuals indicated little feeding activity, but some cannibalism was evident. The only recognizable items were euphausiid ommatidia and other optic material. Of the 1,304 specimens examined; 81.1% had empty food baskets, 17.6% contained euphausiid ommatidia, and the remainder contained unrecognizable material.

Suctorian protozoans infested the exoskeletons of 75.2% of the euphausiids examined.⁶ The thoracic cavity of three female individuals each contained a single larval nematode, identified as *Anisakis* sp.⁷

DISCUSSION

The results provide evidence of sexual segregation in *T. spinifera* and strongly indicate that swarming is related to reproduction. It is unlikely that the euphausiids were transported to the surface by some physical force, judging from the stratified temperature profiles and mild oceanographic conditions, and we found no evidence that they were there to feed or avoid predators.

Some of these findings are very similar to those of others who have recently studied daytime swarming of temperate water euphausiids on other coasts. Nicol (1984a) found that reproductive adults dominated swarms of *Meganyctiphanes norvegica* in the Bay of Fundy, and that sex ratios from patch to patch were highly skewed. He also found a high degree of suctorian infestation in swarm samples

⁶ Identified by S. K. Johnson, Texas A&M University, 111 Nagle Hall, College Station, Texas 77843, pers. commun. May 1986.

⁷ Identified by Mike Moser, University of California, Santa Cruz, CA 95064, pers. commun. April 1986.

compared to those taken at depth offshore (Nicol, 1984b). Endo (1984) and Endo et al. (1985) concluded that swarming of *Euphausia pacifica* in Sendai Bay, Japan, was related to reproduction, although the majority of ripening females they sampled were as yet unfertilized. They also found a predominance of euphausiid spines and eye parts in guts of swarm individuals and a similar infestation of suctorian epibionts.

Adult male euphausiids and the larger adult females may segregate by sex to facilitate schooling (Nicol, 1984a). Those patches in which the sexual segregation was not pronounced may represent the convergence of male and female aggregations and, indeed, swarm patches have been seen to merge and separate.⁸ The fertilized mature females and sexually mature males are assumed to represent the 1983 year class because they correspond to individuals classified as Age 2 by Nemoto (1957). If so, the smaller developing females are likely sexually precocious individuals of the 1984 year class. Their association with the more sexually advanced males may be based on corresponding size and therefore swimming efficiency, rather than corresponding reproductive stage.

Surface swarming may relate to reproduction in one or more of the following ways: (1) for more effectual transfer of spermatophores from males to females, (2) for release of eggs at the surface, or (3) for maturation of sexual products in adults and/or incubation of eggs in warm surface layers. There are arguments for and against all of these possibilities.

Swarming for the purpose of spermatophore transfer seems likely, considering the range of sex ratios in individual patches and observations of swarms merging. But the virtual absence in our samples of mature but as yet unfertilized females suggests otherwise. We have also found a similar absence of unfertilized females in plankton samples and chinook salmon (*Oncorhynchus tshawytscha*) gut contents collected throughout the swarm season. This suggests that the bulk of spermatophore transfer takes place prior to the surface swarming season, and that refertilization of molted females, if it does occur, takes place in areas less accessible to our collecting gear and to salmon predation. Nicol (1984a) also found very few unfertilized mature females in swarming *Meganyctiphanes norvegica* in the Bay of Fundy.

Although the intermolt period for nonreproductive *T. spinifera* has been estimated at 5 to 6 days (Jerde and Lasker, 1966), molting may be delayed or suspended during the reproductive period or upon reaching sexual maturity (Dexter, 1977; Nicol, 1984b). This would further explain why an overwhelming majority of females carry intact spermatophores throughout the breeding season, and may account for the high incidence of exoskeleton infestation by suctorians. Suspension of ecdysis would seem an adaptive means to alleviate the need for segregated males to relocate and refertilize females with each molt.

The presence of eggs in the swarm area suggests that egg release may be an important function of swarming. This hypothesis is supported by the reports of swarms composed entirely of spent female *T. spinifera* (Boden et al., 1955; Percy and Hosie, 1985). Egg incubation, however, is probably not a factor, since euphausiid eggs, being denser than seawater, tend to sink when broadcast freely in the sea (Mauchline and Fisher, 1969). Even so, neritic species such as *T. spinifera* would benefit from releasing eggs high in the water column, thus providing more time for eggs to develop and hatch before reaching the sea floor. After hatching, the larvae are thought to ascend to surface waters where food supplies are abundant

⁸ Peggy Gamin, vessel *Salty Lady*, Harbor Drive, Sausalito, CA 94965, pers. commun. May 1985.

(Mauchline and Fisher, 1969) and the greater average velocity of surface currents can disperse them away from the area and potential cannibalism by adults. But the advantage gained by suspending or reversing normal diel migratory behavior by aggregating at the surface during daylight hours is still not clear. As with other breeding-related activity, egg release could occur during crepuscular or nocturnal periods, presumably with the same benefits mentioned above with the added protection from diurnal predators that darkness would provide. In addition, less than 1% of females in our swarm samples were spent, which indicates that egg release may not be the primary swarm activity during the day, or at least during the afternoon period that we sampled.

Perhaps one of the functions of daytime surface swarming is to prolong exposure of reproductive individuals to the warmer surface layers, where maturation of sexual products would be accelerated. Lindley (1978), working with *Thysanoessa longicaudata*, found that timing of reproduction in spring was correlated with sea surface temperature, and concluded that the rate of sexual maturation is controlled mainly by temperature. The animals may take advantage of interim warming periods between upwelling events to accelerate gonadal development in the warm surface layers. But again, the advantage gained by this strategy would have to outweigh the disadvantage of being highly vulnerable to predation at the sea surface during the day.

Most likely, the adaptive significance of *Thysanoessa spinifera* surface swarming encompasses more than just one factor, since the selective forces acting upon breeding adults would differ from those acting upon eggs and larvae (Dingle, 1980). Both the timing of sexual maturation and the timing of egg release and subsequent larval dispersal would seem crucial, since these events occur during the upwelling season when water temperature and sea surface current velocity and direction can change over a short period of time. Success, however, would seem to depend largely on the rapid behavioral responses of breeding adults. Swarming may be such a response. Although the cost of being at the surface in daylight would seem high for adults because of their greater visibility, the intermittent formation of dense schools, and the rapid response to stimuli that schooling facilitates, may offer the needed edge over predators to ensure that sufficient numbers of adults survive to breed and release their eggs under favorable environmental conditions. The small-scale patchiness revealed by this study re-emphasizes the importance of direct sampling of these reproductive swarms, the dynamics of which may be masked by more conventional sampling with towed plankton nets.

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LITERATURE CITED

- Aitken, J. J. 1960. Swarming in *Meganyctiphanes norvegica* (M. Sars) in Strangford Lough, Co. Down. Ir. Nat. J. 13: 140-142.
- Alton, M. S. and C. J. Blackburn. 1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen, in coastal waters of Washington. Calif. Fish Game 58: 179-190.
- Bakun, A. 1975. Daily and weekly upwelling indices, West Coast of North America, 1967-73. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693. 114 pp.
- Barham, E. G. 1956. The ecology of sonic scattering layers in the Monterey Bay area, California. Ph.D. Thesis, Stanford Univ., Palo Alto, Calif. 182 pp.
-

- Boden, B. P., M. W. Johnson and E. Brinton. 1955. The Euphausiacea (Crustacea) of the North Pacific. Bull. Scripps Inst. Oceanogr. Univ. Calif. 6: 287-400.
- Bolin, R. L. and D. P. Abbot. 1962. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Ocean. Fish. Invest. Rep. IX: 23-44.
- Brinton, E. 1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. Univ. Calif. 8: 51-270.
- Brown, R. G. B., S. P. Parker and D. E. Gaskin. 1979. Daytime surface swarming by *Meganyctiphanes norvegica* (M. Sars) (Crustacea, Euphausiacea) off Briar Island, Bay of Fundy. Can. J. Zool. 57: 2285-2291.
- Dexter, B. L. 1977. The molting biology and molting behavior of two species of euphausiids off Oregon. M.S. Thesis, Oreg. State Univ., Corvallis. 158 pp.
- Dingle, H. 1980. Ecology and evolution of migration. Pages 1-101 in S. A. Gauthreaux, Jr., ed. Animal migration, orientation, and navigation. Academic Press, Inc., New York.
- Endo, Y. 1984. Daytime surface swarming of *Euphausia pacifica* (Crustacea: Euphausiacea) in the Sanriku coastal waters off northeastern Japan. Mar. Biol. (Berl.) 79: 269-276.
- , Y. Hanamura and A. Taniguchi. 1985. In situ observations on the surface swarm of *Euphausia pacifica* in Sendai Bay in early spring with special reference to their biological characteristics. Mer (Tokyo) 23: 135-140.
- Forsyth, D. C. T. and L. T. Jones. 1966. Swarming of *Thysanoessa longicaudata* (Kroyer) (Crustacea, Euphausiacea) in the Shetland Islands. Nature (Lond.) 212: 1467-1468.
- Hatfield, S. E. 1983. Distribution of zooplankton in association with Dungeness crab, *Cancer magister*, larvae in California. Pages 97-123 in P. W. Wild and R. N. Tasto, eds. Life history, environment and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis of the central California fishery resource. Calif. Dep. Fish Game Fish Bull. 172.
- Hopkins, T. L., R. C. Baird and D. M. Milliken. 1973. A messenger-operated closing trawl. Limnol. Oceanogr. 18: 488-490.
- Jerde, C. W. and R. Lasker. 1966. Molting of euphausiid shrimps: shipboard operations. Limnol. Oceanogr. 11: 120-124.
- Komaki, Y. 1967. On the surface swarming of euphausiid crustaceans. Pac. Sci. 21: 433-448.
- Lindley, J. A. 1978. Population dynamics and production of euphausiids. I. *Thysanoessa longicaudata* in the North Atlantic Ocean. Mar. Biol. (Berl.) 46: 121-130.
- Marr, J. W. S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Rep. 32: 33-464.
- Mauchline, J. 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18: 681 pp.
- and L. R. Fisher. 1969. The biology of euphausiids. Adv. Mar. Biol. 7: 454 pp.
- Nemoto, T. 1957. Foods of baleen whales in the northern Pacific. Sci. Rep. Whales Res. Inst. Tokyo 12: 33-89.
- Nicol, S. 1984a. Population structure of daytime surface swarms of the euphausiid *Meganyctiphanes norvegica* in the Bay of Fundy. Mar. Ecol. Prog. Ser. 18: 241-251.
- . 1984b. *Ephelota* sp., a suctorian found on the euphausiid *Meganyctiphanes norvegica*. Can. J. Zool. 62: 744-745.
- Paulsen, O. 1909. Plankton investigations in the waters around Iceland and the North Atlantic in 1904. Medd. Komn Havunders., Ser. Plankton 1(18): 1-57.
- Pearcy, B. and M. Hosie. 1985. Mass stranding of krill off Bandon. Oregon Wildlife. p. 14.
- Ponamareva, L. A. 1966. The euphausiids of the North Pacific, their distribution and ecology. Doklady Akad. Nauk. SSSR, 1-142. Israel Programme for Scientific Translation, Jerusalem.
- Terazaki, M. 1980. Surface swarms of a euphausiid *Euphausia pacifica* in Otsuchi Bay, Northern Japan. Bull. Plankton Soc. Jpn. 27(1): 19-25.

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